Investigating the phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European populations

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Abstract

Recent evidence supports the existence of a downstream autumn migratory phenotype in juvenile anadromous brown trout (*Salmo trutta*), however the precise timing, extent and ecological significance of such behaviour remains ambiguous. We investigated the phenology of downstream migration of wild juvenile trout using passive integrated transponder (PIT) telemetry over an eight month period in two European rivers; the River Deerness, north-east England, and the River Villestrup, Denmark. The incidence of autumn-winter seaward migration was greater in the Deerness than the Villestrup, with at least 46 % of migrating juveniles detected prior to spring smoltification in the Deerness. Timing of migration was strongly regulated by factors associated with river discharge in both systems. While autumn and spring downstream migrants did not differ in size at the time of tagging in either system, evidence that spring migrants were of better condition, travelled faster (autumn: 11.0 km day^{-1}; spring: 24.3 km day^{-1}) and were more likely to leave the Deerness suggests autumn and spring migrant conspecifics respond to different behavioural motivations. Further investigation into the sex of autumn migrant juveniles, as well as the temporal and geographical variability in the incidence and fitness consequences of autumn emigration by juvenile trout would be beneficial.

Keywords: Autumn migration, smolt, ~~*Salmo trutta,*~~ life history, phenotype, phenology, telemetry

Introduction

Individuals of migratory species often exhibit wide variation in their spatial behaviour, varying from local residency to large-scale migration (Nathan et al. 2008; Chapman et al. 2011~~; Dingle, 2014~~), including for fishes (Lucas & Baras, 2001). The literature concerning such variation within the Salmonidae is voluminous (~~–~~reviewed in Dodson et al. 2013). The brown trout, *Salmo trutta* L., exemplifies such phenotypic plasticity with its spatial and temporal continuum of alternative migratory tactics, from locally-resident to potamodromous and anadromous forms (Jonsson & Jonsson, 2011; Boel et al. 2014). Partial and differential migration, at the intrapopulation level, have been illustrated in numerous *S. trutta* populations, notably around Vangsvatnet Lake, Norway (Jonsson, 1985), in the Oir River, France (Cucherousset et al. 2005) and with regard to the extent of marine migration (del Villar-Guerra et al. 2013; Aarestrup et al. 2014).

Despite thorough accounts of behaviour, elements of juvenile salmonid space use and phenology of downstream migration remain poorly explained. It is traditionally considered that juvenile populations of anadromous brown trout and closely related Atlantic salmon, *S. salar*, remain in their native stream from one to several years before descending the river course as smolts in spring (Klemetsen et al. 2003). Therefore, when considering anadromous salmonid population dynamics, the freshwater output of a river typically refers to the production of spring migrants (Ibbotson et al. 2013). Estimates of juvenile salmonid population density are usually carried out in late spring when site fidelity is regarded as strong (Cunjak 1992) and one is typically unable to distinguish mortality from emigration when examining population losses over autumn and winter. Few published tracking or trapping studies have targeted juvenile trout outside spring (but see Jonsson & Jonsson, 2002, 2009; Marine Institute, 2014; Holmes et al. 2014; Taal et al. 2014). For example, in widely cited studies on trout migration, Elliott (1986, 1994) did not investigate evidence that small-scale emigration of Age 1+ trout parr from Black Brows Beck, NW England, appeared to occur year round and represented a high proportion, relative to spring smolt numbers.

Comment [EW1]: I'm not sure whether this sentence is a little redundant.

Comment [M2]: Emily, leave this in. It is a real issue and problem – that was discussed specifically at a meeting I was recently. So keep that sentence in please.

Downstream movements of *S. salar* juveniles are well known in autumn (Youngson et al. 1983; Cunjak et al. 1989; Pinder et al. 2007; McGinnity et al. 2007; Jensen et al. 2012; Jonsson & Jonsson, 2014; Taal et al. 2014), although the proportions of populations undertaking those movements, and their significance, are~~is~~ still not fully understood. By contrast, autumn descents of immature brown trout have been less widely recorded, but information is available in Irish (Marine Institute, 2014), Norwegian (Jonsson & Jonsson, 2002, 2009), Baltic (Taal et al. 2014) and New Zealand (Holmes et al. 2014) populations. Based upon population-specific interpretations of phenotype, non-moribund, juvenile salmonid autumn migrants are regarded as pre-smolts, destined to enter the sea (McGinnity et al. 2007), or as comprising potamodromous population components that may be common in larger river systems (Cucherousset et al. 2005). Survival may also differ by population, for example the weakly brackish environment encountered by autumn migrants in the Baltic Sea does not require marine-level osmoregulatory competency for survival (Taal et al. 2014). Alternatively,~~, but~~ ice, low river discharge and the absence of an estuary in which to reside are thought to cause poor survival of *S. salar* autumn migrants leaving the River Halselva, Norway and a lack of sympatric *S. trutta* conspecifics (Jensen et al. 2012). Autumn migrant *S. salar* do not appear suitably adapted to seawater (Riley et al. 2008), and sea survival rates of first-time, autumn-emigrant *S. trutta* in Norway are significantly lower than those in spring (Jonsson & Jonsson, 2009), however the viability of these phenotypes has been confirmed with returning *Salmo* adults (Jonsson & Jonsson, 2009; Riley et al. 2009).

Despite enhanced awareness of an autumn downstream migratory phenotype in juvenile salmonids over recent years, our understanding of its ecological significance remains limited and somewhat contested. Recorded incidence of autumn migration has been associated with proximity to the marine environment (Ibbotson et al. 2013), elevated stream discharge (Youngson et al. 1983) and poor overwintering habitat (Riddell & Leggett, 1981), as well as the reproductive motivations of precociously mature male parr (Buck & Youngson, 1982; McGinnity et al. 2007; Jensen et al. 2012). Holmes et al. (2014) suggested that early emigration of larger trout parr from the Rainy River, New

Zealand reflected limited overwintering habitat availability and/or constrained feeding opportunities for individuals with high growth rates. Determining the value of alternative wintering habitats, in terms of trout survival, smolt output, performance in the sea and ultimately their fecundity , is important for river and fisheries managers in directing conservation, regulation and habitat management (Ibbotson et al. 2013), such as when considering the importance of year-round downstream fish passage.

Comment [EW3]: Maybe I'm being too ruthless by cutting this…

Comment [M4]: I agree this sentence could be cut

In this study we examined and compared the phenology of downstream migration in two juvenile trout populations in north-east England and Denmark, using Passive Integrated Transponder (PIT) telemetry. We investigated the influence of environmental, subject-specific and tag-site specific variables on the probability of passage past fixed monitoring sites over an eight month period.

Materials and Methods

Study areas

The River Deerness (mean annual discharge ~0.5 m^3s^{-1} in its lower reaches) is a small tributary (width in study reaches, 2-10 m) of the River Browney in NE England (54°44' N, 1°48' W) and flows into the North Sea via the River Wear (Fig. 1). The Wear has large stocks of Atlantic salmon and sea trout with annual resistivity (partial) counts of upstream adult migrants at Durham, 29 km from the sea, averaging 15,593 fish per year between 2007 and 2014 (Environment Agency, 2015). The Deerness drains a catchment of 52.4 km^2, and is 16.3 km long, consisting largely of grassland to the west, and transitioning to woodland and lower-lying arable areas in the east. The brown trout population consists of multiple cohorts, with a mixture of resident and migratory adults, including anadromous trout (E. Winter, J. Tummers unpublished data).

The River Villestrup (56°46' N, 9°55' E) is the primary freshwater source for the strongly brackish Mariager Fjord, ultimately exchanging with the Kattegat Sea on the east coast of Jutland, Denmark (Fig. 1). The river has a mean annual discharge of 1.1 m^3s^{-1}. The Villestrup is approximately

20 km long, has a typical width in the studied reach of 4-10 m and drains a catchment of 126 km^2. The average density of wild 0+trout is estimated at 125 per 100 m^2 (HELCOM, 2011). No stocking occurs. The inner fjord has salinities of 12-17 PSU in the upper 10 m of the water column used by trout, while deeper areas are more saline but often hypoxic. The shallow outer fjord has salinities of 20-25 PSU. The Villestrup joins near the junction between the inner and outer fjord areas, on the north shore (Fig. 1).

PIT tagging, recapture and telemetry

Trout in the Deerness system were captured for PIT-tagging using electric-fishing equipment at six sites dispersed over *ca.* 15 km of stream length (Fig. 1). Tagging occurred between 9 July and 12 September 2014 (*n* = 643), with a small number (*n* = 23) also tagged on 6 November 2014 (mean FL ± SD of all trout = 151 mm ± 23). In the Villestrup, trout were tagged on 26 September 2014 (*n* = 490; mean FL ± SD = 147 mm ± 27), using electric-fishing in a single reach *ca.* 8.5 km upstream of the river outlet (Fig. 1). Parr ≥120 mm (Larsen et al. 2013) and ≤250 mm from each study area were anaesthetised (Deerness: buffered MS-222, 100 mg L^{-1}; Villestrup: Benzocaine, 25 mg L^{-1}), weighed (to 0.1 g), measured (fork length, FL to 1 mm) and surgically implanted with a PIT-tag (Texas Instruments; model RI-TRP-RRHP, HDX, 134.2 kHz, length 23.1 mm, diameter 3.85 mm, weight 0.6 g in air). Tags and instruments were disinfected with 90% ethanol and air dried before use. Procedures were carried out by an experienced fish surgeon and following local animal welfare regulations. Following recovery, all individuals were returned to their site of capture. Recapture methodology used to investigate summer dispersal on the Deerness is presented in Online Resource 1.

Three pairs of stream-width swim-through half-duplex (HDX) PIT antennae were installed on a 5 km stretch of the lower Deerness (Fig. 1; Bolland et al. 200910), operational from 24 September 2014 at stations M2 and M3 and 13 October at station M1 (Fig. 1), until 31 May 2015. Due to occasional battery failure and a damaging high flow event in November causing severe loss of efficiency, the stations M1, M2 and M3 were operational 95.6, 98.1 and 98.1 % of the time,

130 respectively. On the Villestrup, a single pair of mains-powered antennae were placed 300 m
131 upstream of the river outlet (Fig. 1), functional 88.7 % of the time from 26 September 2014 to 31
132 May 2015. Tags were detected by time-synchronised Master and Slave HDX readers (Texas
133 Instruments SX2000; in-house build), interrogating the pairs of antennae eight times per second
134 (Castro-Santos et al. 1996). Detection ranges between 20 and 80 cm were achieved and correct
135 function on the Deerness was confirmed by passing a test tag through each antenna before and after
136 each battery change (every 4 ± 2 days), and by more detailed range testing periodically. Each
137 Villestrup antenna had a timed auto-emitter check tag (Oregon RFID). Additionally on the Villestrup,
138 a Wolf-type trap (Wolf, 1951) situated directly downstream of the PIT antennae captured migrating
139 smolts from 18 March 2015 until the end of the study. For the purpose of this study, and by
140 reference to standard terminology applied elsewhere (e.g. Ibbotson et al. 2013), all fish detected
141 prior to 1 February were labelled autumn migrants, while those detected from 1 February to 31 May
142 were labelled spring smolts.

143 Theoretical antenna efficiencies of 99, 100 and 100% were achieved for stations M1-3,
144 respectively, by routinely passing a test tag through the system. In practice, several factors influence
145 a tag's probability of detection, including environmental conditions, tag velocity, tag orientation and
146 the presence of other tags (Zydlewski et al. 2006; Burnett et al. 2013). A practical estimate of
147 efficiency is, hence, given by the ratio of fish detected at a site that are known to have passed
148 through (Zydlewski et al. 2006), and was estimated at 98.4% for M2. The efficiencies of M1 and M3
149 could not be estimated using this method, due to the absence of detection equipment downstream
150 and the time lag between tagging events and the onset of monitoring, meaning the location of
151 individuals prior to detection was uncertain. Using Zydlewski et al.'s (2006) method, the efficiency of
152 the Villestrup station was estimated as 86.5% in spring, by identifying individuals caught in the
153 downstream trap that were not detected by the PIT antennae.

154 *Population density estimations and environmental monitoring*

155 Quantitative estimates of trout densities (n·100 m^{-2}) were made at each of the Deerness
156 tagging sites, using a multiple-pass depletion method (Carle & Strub, 1978) in July 2014 (average
157 triple-pass catchability 97.2% for ≥ Age 1) and subsequently in March 2015 (average triple-pass
158 catchability 98.4% for ≥ Age 1). Developmental state of recaptured individuals (parr, smolt [including
159 part-smolt] or adult) was also recorded, based on phenotypic characteristics (e.g. parr marks, body
160 colour, body shape; Tanguy et al. 1994), in order to predict the seaward movement of certain
161 individuals.

162 One logger (HOBO®; model U20-001-01; Onset Computer Corporation), situated at M3 on the
163 Deerness, recorded temperature (accuracy ±0.4 °C) and water pressure (accuracy ±0.6 kPa,
164 converted to river level) at 15-min intervals throughout the study. On the Villestrup, temperature
165 was measured at the upper antenna (Tinytag plus 2; model TGP-4017, www.geminidataloggers.com)
166 and water level records were obtained from a fixed gauging station ca. 1 km upstream of the river
167 outlet (Fig. 1).

168 *Statistical analyses*

169 The influence of environmental factors on the timing of downstream movement was analysed
170 using generalised linear models (GLMs), comparing daily detection frequency with fluctuations in
171 average daily water temperature (°C), photoperiod, average daily water level (m) and the change in
172 average daily water level (m). Initial Poisson GLMs revealed non-linear residual patterns and
173 overdispersion, which was corrected for using the negative binomial distribution with a log-link
174 function (Richards, 2008). All combinations of explanatory variables were trialled, but never utilising
175 collinear factors (e.g. temperature and photoperiod). Following this, we explored the effects of
176 subject-specific variables on the probability of tagged trout being detected as autumn or spring
177 migrants. Binomial GLMs with a cloglog link function, due to asymmetry in the numbers of migrants
178 and non-migrants, were constructed using combinations of the independent factors fish length
179 (mm), mass (g) and Fulton's condition factor, but never with collinear variables (e.g. length and

mass). The additional variables tag-site density (n·100m^{-2}, summer 2014), tag-site distance upstream (km), and date of tagging were also analysed for subjects on the Deerness. Twelve Deerness fish, one a spring migrant, one an upstream migrant and ten undetected, and two Villestrup fish, one a spring migrant and one undetected, were omitted from this analysis due to a lack of mass, and hence condition, records. All analyses were conducted in R 3.1.1 (R Core Team, 2014) with use of the MASS package (Venables & Ripley, 2002). Model selection followed the minimisation of Akaike's information criterion (AIC) values, which represents the best compromise between lack of precision (too many parameters) and bias (too few parameters). Models within Δ6 AIC were retained, provided they were not increasingly complex versions of more efficient nested counterparts (outlined by Richards, 2008).

For further examination, we used independent-sample *t*-tests to compare the average length, mass, condition factor and net ground speed (km day^{-1}) of autumn and spring migrating individuals. Chi-squared tests with Yates' continuity correction were used to determine if the proportion of Deerness fish caught, inspected and categorised as smolts in March and subsequently detected downstream differed by tag site, and if the proportion of Deerness downstream migrants reaching M1 differed between autumn and spring.

Results

Site fidelity was strong during summer 2014, with 83% of recaptured Deerness trout parr (*n* = 330) travelling no further than 60 m and < 0.01% travelling over 200 m, from a previous known site of release (Online Resource 2). From autumn onwards, 140 (21.0%) of the 666 Deerness trout were PIT detected downstream of the site at which they were tagged and released, comprising 83 autumn migrants, 52 spring migrants and five individuals with activity spanning both periods (from here on labelled autumn migrants). Trout detected at M1 were assumed to have left the Deerness system, comprising 89 individuals in total (13.4%), 41 in autumn and 48 in spring. Migratory behaviour was observed throughout the period of study, with peaks of activity in October, November, March and

May (Fig. 2). Eleven upstream migrants from T1 to M3 were recorded, all occurring in autumn and none of which were detected leaving the stream. In March 2015, parr densities had decreased at all but one of the tagging sites (Table 1), by an overall average of 49%; a total of 50 tagged trout were recaptured in March across all release sites, of which 17 subsequently migrated downstream.

In the Villestrup, 195 of 490 tagged trout (39.8 %) were detected at the monitoring site and/or caught in the trap, comprising 49 autumn migrants, 136 spring migrants, and ten individuals with activity spanning both periods (from here on labelled autumn migrants). The Villestrup trout did not display a distinct autumnal peak of activity, however low levels of migratory behaviour were sustained throughout autumn and winter months. Activity of spring smolts peaked in late March, with continued high levels of movement throughout April and early May (Fig. 2).

Environmental regulators of downstream migratory behaviour

Mean daily water temperature and water level were retained in the best model for predicting autumn migrant activity in the Deerness (Table 2), both sharing significant positive relationships with daily detection frequency. No other combinations of variables were retained under the selection criteria, reflecting their poor explanatory power. In contrast, the change in mean daily water level was the best predictor of spring migrant activity in the Deerness, with a significant positive relationship. Two further models were retained utilising the variables water level and photoperiod, however greater ΔAIC values signified weaker explanatory power (Table 2). The best model predicting autumn migrant activity in the Villestrup retained both water level and temperature, but, in contrast to the Deerness, with a significant negative effect of temperature (Table 2). Under the selection criteria, five models were retained for predicting spring migrant activity in the Villestrup, with the best predictors being change in mean daily water level and water temperature in positive trends (Table 2). The removal of temperature produced a model with a ΔAIC of 0.3, indicating the explanatory power of temperature is low and water level on its own is a powerful predictor of daily smolt counts.

230 *Phenotypic determinants of downstream migratory tendency*

231 The best model describing autumn migrant probability in the Deerness retained fish mass and
232 tag site distance upstream as predictive parameters, both with significant negative trends (Table 3;
233 Fig. 3). Three alternative models utilising combinations of length, condition, distance and date can
234 be found in Table 3. The best model for predicting spring migration retained subject mass, condition
235 factor and tag site distance upstream. Mass and tag site distance shared significant negative
236 relationships with probability of spring detection, while condition factor shared a positive
237 relationship (Table 3; Fig. 3). Notably, tag site distance was retained in all models for the Deerness,
238 suggesting it is a strong predictor of migratory tendency for all downstream migrating juveniles, but
239 particularly for spring smolts, given the higher coefficient estimates. This is supported by
240 significantly more smolts (captured, inspected and classified in March 2015) than expected being
241 detected originating from T1, the most downstream tag site, relative to sites further upstream (Chi-
242 square: $\chi^2_1 = 6.18$, $p = 0.013$). Autumn and spring migratory tendency in the Villestrup were best
243 predicted by fish mass and condition, both sharing negative relationships in each scenario (Table 3;
244 Fig. 3). For the autumn migrants, mass was a particularly strong predictor on its own, given the
245 removal of condition to produce a model with a ΔAIC of only 0.7.

246 *Comparisons of migratory phenotypes*

247 There was no difference in length ($t_{138} = 0.22$, $p = 0.82$) or mass ($t_{137} = 0.39$, $p = 0.70$) at the time
248 of tagging between autumn and spring migrants in the Deerness; however there was some evidence
249 to suggest condition factor was greater in spring migrants ($t_{137} = 2.00$, $p = 0.048$; Fig. 3). Mean length
250 and mass of upstream migrants was also significantly greater than that of all downstream migrants
251 in the Deerness (Length: $t_{149} = 3.55$, $p < 0.001$; Mass: $t_{147} = 4.62$, $p < 0.001$; Fig. 3), although we found
252 no difference in condition factor ($t_{147} = 0.05$, $p = 0.96$). There was no difference in length ($t_{193} = 0.12$,
253 $p = 0.90$), mass ($t_{192} = 0.26$, $p = 0.79$) or condition factor ($t_{192} = 0.32$, $p = 0.75$; Fig. 3) between autumn
254 and spring migrants in the Villestrup. Individual net ground speed of downstream migrants in the

Deerness varied dramatically from less than 1 to 88 km day^{-1} throughout the study period, but on average, spring migrants travelled significantly faster (24.3 km day^{-1}) than autumn migrants (11.0 km day^{-1}) (t_{127} = 3.82, p < 0.001; Fig. 4). Additionally, downstream migrants were classified as stream 'emigrants' following a final detection at the most downstream monitoring site, *ca.* 700 m from the Deerness' confluence with the river Browney. A significantly greater proportion of spring migrants (84.6%) than autumn migrants (49.4%) became stream emigrants during the period in which they were first detected (Chi-square: χ^2_1 = 15.5, p < 0.001). Five autumn non-emigrants were subsequently detected in the spring, four of which were then detected moving past M1.

Discussion

Extensive autumn downstream migrations were evident in juvenile brown trout (*Salmo trutta*) for both the Villestrup (Jutland, Denmark) and the Deerness (north-east England). Over 1.5 times the number of spring smolts were observed active between October and January in the Deerness. Moreoverthose leaving the system during autumn-winter represented 46% of all stream-emigrant juveniles in the study period. This contrasts the strong site fidelity observed during summer months and provides quantitative evidence of the protracted overwinter nature of the downstream migratory behaviour, broadly similar to that of the Marine Institute (2014), which states numbers of autumn migrating juveniles in the Burrishoole catchment, Ireland, have fluctuated between 18% and 57% of the total annual juvenile downstream migrant count, since 1982. Both the Burrishoole and Deerness catchments are characterised by mild, oceanic climates and frequent flow elevations following rainfall, possibly accounting for the prolonged 'autumn' downstream migration. Nevertheless, Deerness migrants cannot fully account for the marked reduction in parr densities at sites T2-T5 by March 2015, which must also reflect either local movement outside tagging sites, low overwinter survival, or a combination of both.

Probability of migration was higher in the Villestrup, but incidence of autumn migration was lower (25% of the total juvenile stream-emigrant count), yet remains higher than that reported by

Jonsson and Jonsson (2009) in Norway. Migrants in the Villestrup are assumed to enter the brackish Mariager Fjord soon after passage through the PIT monitoring station, however autumn migrants may have low gill Na^+K^+-ATPase activity, as observed for autumn-emigrating *S. salar* juveniles (Riley et al. 2008). This could cause osmoregulatory stress, although salmonid parr have been known to reside in estuarine environments (Cunjak et al. 1989; Pinder et al. 2007). Conversely, individuals in the Deerness have much further to travel before reaching a saline environment, (meaning their migration strategy, i.e. anadromy or potamodromy, is unknown), and may explain why incidence of autumn migration is particularly high there. The recognition of an alternative juvenile downstream migratory phenotype is growing internationally and, hence, the potential contribution of these individuals to adult recruitment must be acknowledged.

The environmental factors regulating the phenology of downstream movement of salmonid smolts have been well studied, particularly the behavioural responses to water temperature, flow and light (e.g. Jonsson, 1991; Aarestrup et al. 2002; Aldvén et al. 2015). Stimuli for migration differ in their importance geographically between river systems and temporally between years (Hembre et al. 2001. This study suggests that water level (and hence river discharge) had the greatest influence on autumn migrant movement in both the Deerness and Villestrup, in accordance with Youngson et al. (1983), Jonsson and Jonsson (2002) and Holmes et al. (2014). This is not surprising, given the opportunity to minimise the energetic costs of migration, while high turbidity may offer greater protection from predators (Hvidsten & Hansen, 1989). Th~~In contrast, th~~e change in average daily water level was a better predictor of movement of spring migrants in both the Deerness and Villestrup. This suggests smolts in both systems are particularly receptive to dynamic fluctuations in the hydrograph, similar to Carlsen et al.'s (2004) conclusions that migrating juveniles can anticipate floods. Importantly, all models retained in Table 2 utilised an environmental variable associated with river discharge, suggesting it is a central migratory stimulus for both populations.

304 Autumn migrants in the Deerness and smolts in the Villestrup responded positively to higher
305 temperature, analogous to results obtained by Jonsson and Ruud-Hansen (1985). Smolt activity in
306 the Deerness was better predicted by photoperiod, which is known to regulate physiological changes
307 associated with the parr-smolt transformation (Björnsson et al. 2011). The probability of autumn
308 migration in the Villestrup shared a significant negative relationship with temperature (see also
309 Jonsson & Jonsson, 2002), yet previous studies reporting increased migrant activity at cold
310 temperatures are usually associated with ice melt (Hesthagen & Garnås, 1986; Carlsen et al. 2004).
311 One possibility for the observed pattern is that peak flows may have coincided with low
312 temperatures in winter, demonstrating a degree of behavioural independence with regard to
313 seasonal variables. Also, the Villestrup is spring-fed, meaning temperatures are comparatively more
314 stable to those of the Deerness. The relative importance of temperature, photoperiod and river
315 discharge as migratory triggers may, however, fluctuate between years (Jensen et al. 2012; Aldvén et
316 al. 2015), depending on precipitation and rate of temperature change. Longer-term and
317 experimental studies in either system could reveal variability and mechanisms in the effect of
318 environmental cues.

319 The probability of an individual conducting autumn or spring migration past fixed points on the
320 Deerness decreased significantly in an upstream direction. Ibbotson et al. (2013) proposed a re-
321 distribution of autumn migrating *S. salar* parr in a downstream direction was responsible for similar
322 findings, rather than a targeted migration. One explanation for this may be to consider the potential
323 disturbance caused by environmental events such as high autumn-winter flows. Territorial behaviour
324 may be disrupted, initiating a re-establishment of dominance hierarchies and promoting the
325 downstream displacement of subordinate individuals. While this may hold true for autumn-winter
326 migrants, it is unlikely to be the case for spring smolts, but for which we found a reduced probability
327 of detection from tag sites further upstream. Moreover, there appears no trend in the percentage of
328 recaptured residents with distance upstream (Table 1), which would be expected if migration
329 tendency decreased in an upstream direction. We, therefore, suggest a cumulative increase in

mortality probability with increasing distance upstream for both autumn and spring migrants, for example due to anthropogenic obstruction during migration, greater energetic costs or exposure to predators (Aarestrup & Koed, 2003~~Bohlin et al. 2001~~; Gauld et al. 2013).

In early studies it was hypothesised that anadromous salmonid juveniles migrate at the first opportunity after reaching a threshold size (Elson, 1957; Fahy, 1985), yet for brown trout, smolt length can vary from <100 mm to >200 mm within the same river (Økland et al. 1993). Fast-growing individuals smolt at a younger age and smaller size than their slow-growing counterparts (Forseth et al. 1999). In the Deerness and Villestrup, autumn and spring migratory tendency were negatively affected by body mass, which was always a better predictor than body length. This may be counterintuitive, considering migration and post-migration survival is thought to be positively size-dependent (Bohlin et al. 1993), but could suggest migrating juveniles in these river systems were energetically constrained. Migration has been described as a biological response to adversity (Taylor & Taylor, 1977), and in the Deerness (autumn migrants) and Villestrup (all migrants) migratory tendency was negatively correlated with fish condition at tagging, which could result from adversity in the form of poor growth opportunities. Notably, the optimal size at migration in the Deerness and Villestrup systems could be lower than the size range of individuals sampled such that some of the tagged trout, especially males, may have been maturing.

Comment [M5]: No, I think leave all of this and the references in – I think this is a significant (popular) area of debate and it is relevant to include

Comment [EW6]: Most of the citations given here are only referenced once. Given the comment about too many references maybe some could be removed, but it would mean removing the discussion around them. I'm not sure…

The size of autumn and spring migrants did not differ at the time of tagging in either the Deerness or Villestrup, as found by Ibbotson et al. (2013) for *S. salar*. In contrast, some found autumn migrants to be significantly larger than spring migrants or residents of the same year-class, possibly indicating constrained habitat availability for faster-growing individuals or achievement of a high energy store status (Huntingford et al. 1992; Holmes et al. 2014). This hypothesis is not supported by our results. In the Deerness, spring migrants were of better condition than autumn migrants at the time of tagging and autumn and spring migratory tendencies shared opposed relationships with individual body condition. This may have been a result of competition, such that

355 subordinate individuals with lower body condition were displaced by their dominant counterparts,
356 either preferentially leaving a low-growth potential environment or forced out of refugia with an
357 overwinter reduction in stream carrying capacity (see Keeley, 2001). Migration in brown trout can be
358 regulated by food availability (Wysujack et al. 2008), therefore autumn migrants could result from a
359 competition-induced lack of resources for subordinates. On the contrary, we found no evidence to
360 suggest the density of trout Age 1+ and older at each Deerness site could predict the proportion of
361 autumn migrants. However, caution is needed, since local habitat has been shown to influence the
362 autumnal movement of Atlantic salmon parr, perhaps due to differences in the proximity of
363 overwintering habitat (Ibbotson et al. 2013).

364 Autumn upstream migrants in the Deerness, characteristic of precocious parr maturation
365 (McCormick et al. 1998), were larger than downstream migrants. Precocious parr are predominantly
366 males and the anadromous emigrants' sex ratio is typically heavily skewed towards females
367 (Klemetsen et al. 2003) although autumn downstream migration has been linked to the reproductive
368 motivations of precocious parr (Buck and Youngson, 1982). F~~, but f~~ish sex was unknown in this study,
369 although 22.5% of tagged and untagged parr morphotypes ≥ 120 mm, sampled on the Deerness in
370 November 2014 were spermiating males (E. Winter, unpublished data). Cheap molecular methods
371 for the sexing of juvenile salmonids from tissue samples are now available (Quéméré et al. 2014) and
372 will aid sex-specific interpretation of movement patterns in parr morphotype salmonids.

373 Questions regarding the ecological significance of autumn migration of juvenile salmonids
374 remain. Increased plasma thyroxine levels in autumn migrants are suggestive of a physiologically
375 mediated migration (Riley et al. 2008; Zydlewski et al. 2005), however the behavioural motivations
376 of autumn and spring migrants may differ, since autumn-migrating parr are not physiologically
377 adapted for seawater entry (Riley et al. 2008). Deerness spring migrants travelled at a greater net
378 ground speed, at rates similar to those obtained by Aarestrup et al. (2002) for radio tagged trout
379 smolts, and were more likely to become stream emigrants than autumn migrants. While antennae

malfunction during a major spate in November 2014 may be partially responsible for a lack of autumn detections at M1, these results suggest the movements of Deerness autumn individuals are not exclusively marine-targeted. In the Villestrup it seems likely that downstream-migrating parr recorded at the PIT station at the bottom of the river subsequently enter the Mariager Fjord, though they could remain in the river outlet. It would, therefore, be valuable to determine the range of salinities and temperatures to which juvenile autumn emigrants are exposed and their survival in relation to their physiological readiness for seawater transition.

In conclusion, this study provides quantitative evidence for considerable autumn and winter downstream migration of juvenile brown trout in the rivers Deerness and Villestrup, along with correlative information on factors regulating behaviour, to parallel the wealth of knowledge concerning spring smolt migration. We propose different behavioural motivations for autumn and spring migrants, based on individual condition, the proportion of emigrants and rates of migration for each group in the Deerness. We emphasise the dynamic behavioural nature of the brown trout and suggest the autumn-migratory phenotype represents an important avenue within the migration continuum concept (Cucherousset et al. 2005; Dodson et al. 2013; Boel et al. 2014), dependent on environmental and physiological factors relating to individual fitness. An in-depth, experimental evaluation of the temporal, spatial and genetic variability of the extent of autumn migration of trout, and its influence on subsequent life history traits, would be beneficial to future conservation and management plans.

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Figure legends

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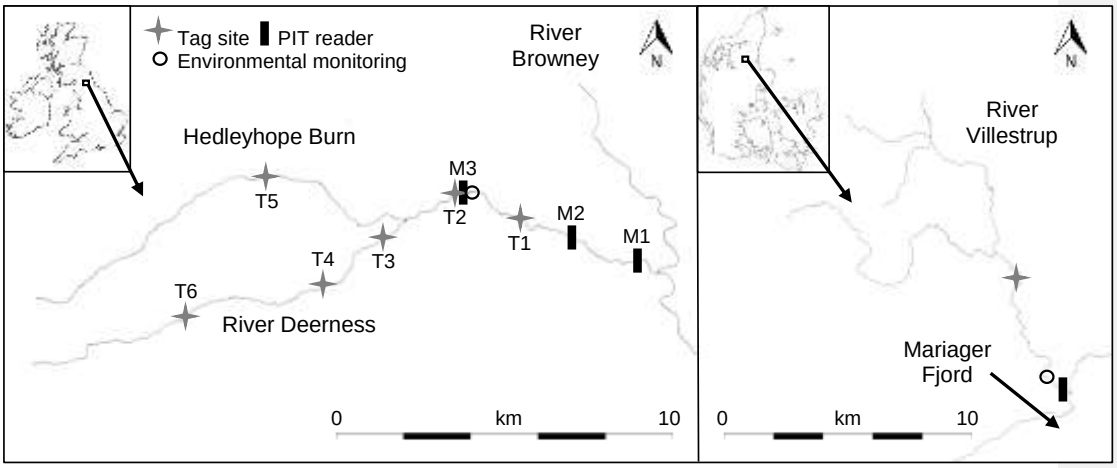
Fig. 1 Map of the Deerness and Villestrup study areas, showing the locations of tagging sites, fixed PIT readers and environmental monitoring stations with stars, thick lines and open circles, respectively. On the Deerness, an environmental monitoring station was also placed at M3. Inset maps show the location of the study areas nationally.

Fig. 2 Daily detection frequency of PIT tagged trout parr detected downstream of the site at which they were tagged and released on the Deerness (a) and Villestrup (c). Date of first detection only is displayed. Shaded regions represent periods of minimal or no detection efficiency due to PIT antennae malfunction. Individuals detected prior to 1 Feb were labelled autumn migrants and those detected from 1 Feb labelled spring smolts following published convention (Ibbotson et al. 2013). In addition, a downstream trap was operational from 18 March on the Villestrup, indicated by the arrow on panel (c). Average daily water temperature (solid lines) and average daily water level (dotted lines) are also displayed for the Deerness (b) and Villestrup (d)

Fig. 3 The mean length, mass and condition factor at tagging (± SEM) of undetected trout, autumn downstream migrants, spring downstream migrants and upstream migrants in the Deerness (top row) and the Villestrup (bottom row)

Fig. 4 The mean net ground speed (± SEM) of autumn and spring migrants in the Deerness.



588

589 Fig. 1

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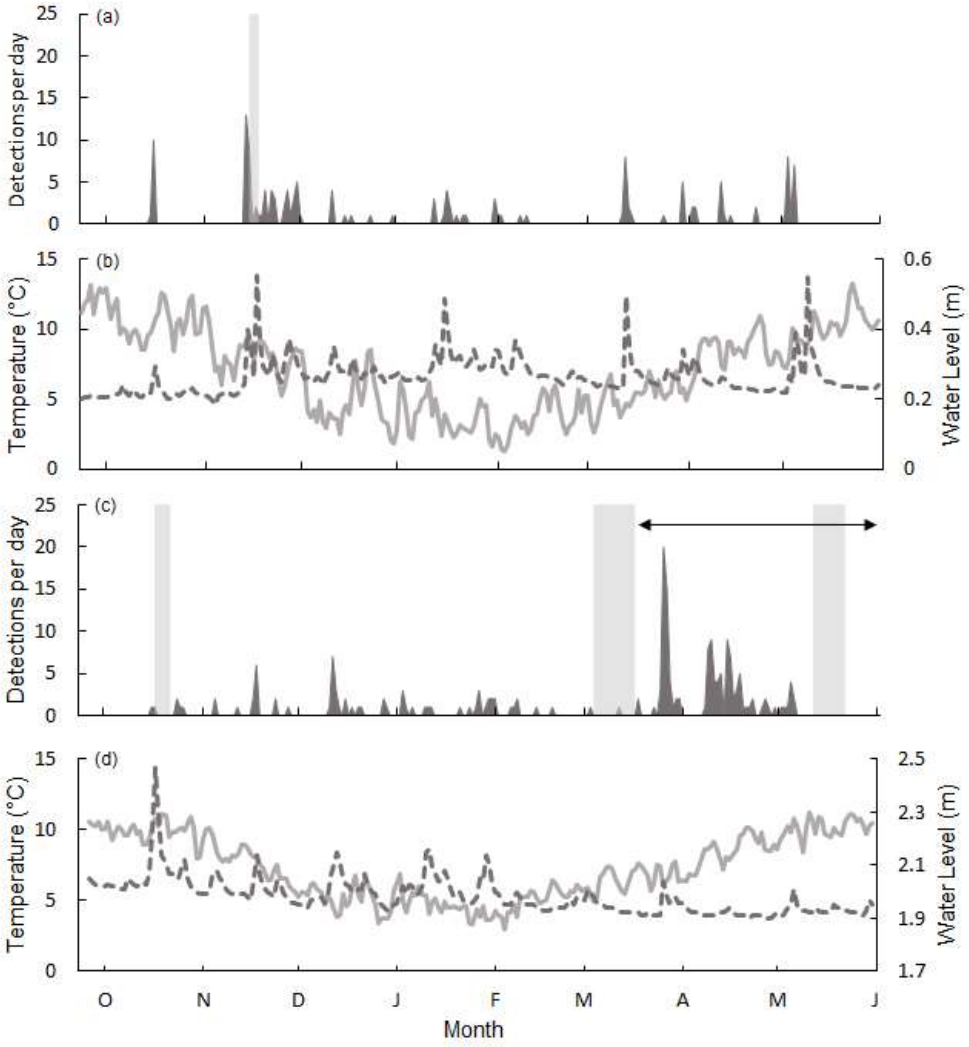

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592 Fig. 2

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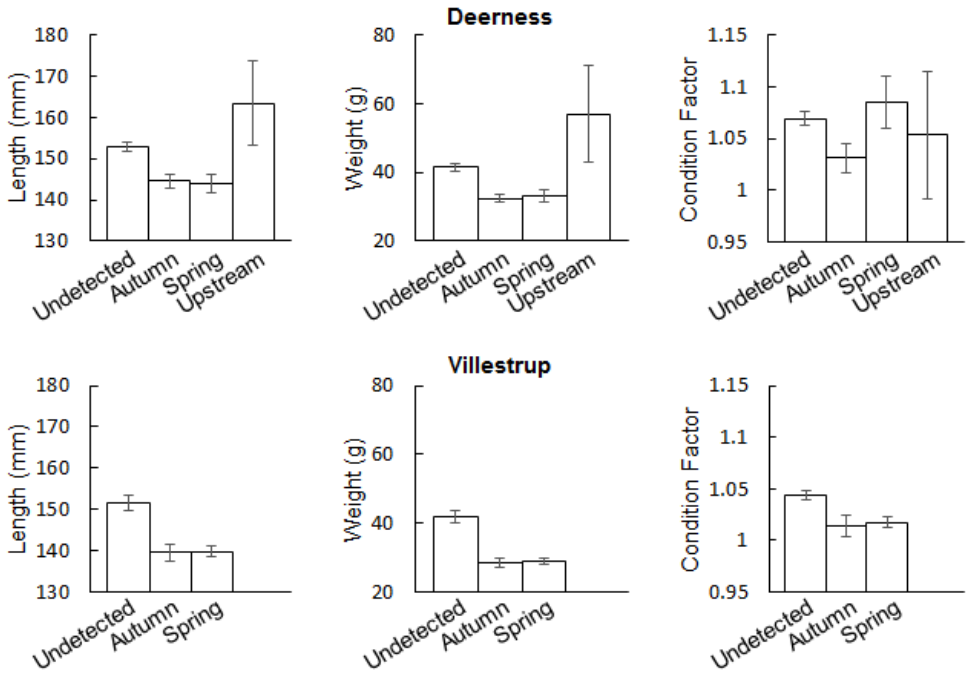
Deerness
Length (mm)
180
170
160
150
140
130
Undetected
Autumn
Spring
Upstream
Weight (g)
80
60
40
20
Condition Factor
1.15
1.1
1.05
1
0.95
Villestrup
Length (mm)
180
170
160
150
140
130
Undetected
Autumn
Spring
Weight (g)
80
60
40
20
Condition Factor
1.15
1.1
1.05
1
0.95
Undetected
Autumn
Spring

Fig. 3

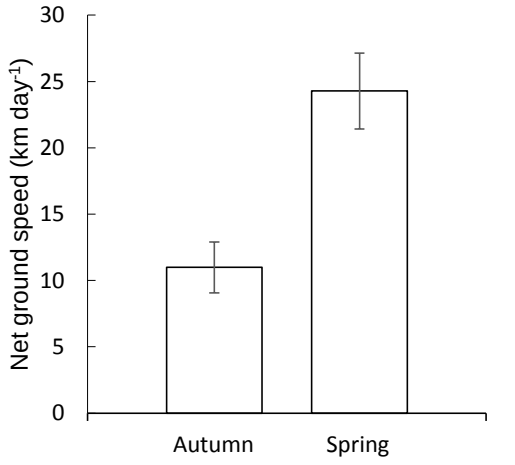
Net ground speed (km day-1)
30
25
20
15
10
5
0
Autumn
Spring

Fig. 4

603 Table 1: Details of tag site-specific variables on the Deerness, along with results of PIT telemetry and March recapture surveys by site.

Tag Site	Distance from river mouth (km)	Density '14 ($n \cdot 100m^{-2}$)	Density '15 ($n \cdot 100m^{-2}$)	%Δ Density	No. fish tagged	% Migrated Downstream	% Recaptured residents	% Loss from mortality or local dispersal
T1	4.2	12.0	14.3	+19.2	214	33.6	4.2	62.2
T2	6.2	9.2	3.7	-59.8	99	10.1	6.1	83.8
T3	8.6	12.2	1.9	-84.4	91	28.6	3.3	68.1
T4	10.8	9.5	1.5	-84.2	55	18.2	7.3	74.5
T5	11.8	12.2	2.3	-81.1	140	12.1	2.1	85.8
T6	14.5	7.7	7.5	-2.6	67	7.5	10.4	82.1

604

605

Table 2: Generalised linear model outputs of migration phenology analyses. All retained models within 6 ΔAIC are displayed. Significant variables are in bold, with values for predictor variables representing coefficient estimates.

Model	AICc	ΔAICc	df	Intercept	Water Level	Δ Water Level	Water Temperature	Photoperiod
Deerness Autumn								
1	202.3	0.0	4	**-12.00**	**33.30**		**0.24**	
Deerness Spring								
1	166.8	0.0	3	**-1.76**		**22.83**		
2	168.3	1.5	4	**-9.51**	**20.24**			**0.004**
3	169.1	2.3	3	**-5.84**	**17.35**			
Villestrup Autumn								
1	207.7	0.0	4	**-20.80**	**10.83**		**-0.34**	
2	208.6	0.9	4	**-18.23**	**11.02**			**-0.011**
Villestrup Spring								
1	311.7	0.0	4	**-1.87**		**27.04**	**0.20**	
2	312.0	0.3	3	-0.26		21.68		
3	316.1	4.4	4	-29.64	13.77			**0.004**
4	316.4	4.7	4	**-34.35**	**16.62**		**0.28**	
5	317.3	5.6	3	-17.57	9.10			

Table 3: Generalised linear model outputs of migration tendency analyses. All retained models within 6 ΔAIC are displayed. Significant variables are in bold, with values for predictor variables representing coefficient estimates.

Model	AICc	ΔAICc	df	Intercept	Length	Weight	Condition	Density	Distance	Days
Deerness Autumn										
1	487.4	0.0	3	0.26		**-0.032**			**-0.136**	
2	489.7	2.3	5	**4.29**	**-0.023**		**-1.86**		**-0.146**	0.006
3	489.7	2.3	4	**3.93**	**-0.022**		-1.42		**-0.137**	
4	491.3	3.9	3	**2.48**	**-0.022**				**-0.143**	
Deerness Spring										
1	340.7	0.0	4	-1.35		**-0.041**	**1.79**		**-0.178**	
2	341.0	0.3	3	**3.42**	**-0.029**				**-0.178**	
3	343.0	2.3	3	0.24		**-0.035**			**-0.164**	
Villestrup Autumn										
1	353.9	0.0	3	2.15		**-0.023**	-3.33			
2	354.6	0.7	2	**-1.21**		**-0.024**				
3	356.0	2.1	3	4.34	**-0.014**		**-4.19**			
4	358.4	4.5	2	-0.002	**-0.014**					
5	359.3	5.4	2	2.34			**-4.22**			
Villestrup Spring										
1	527.0	0.0	3	**4.70**		**-0.026**	**-4.42**			
2	532.6	5.6	3	**7.40**	**-0.017**		**-5.47**			

Online Resource 1: Investigating the phenology of downstream migration in juvenile trout.

Methodology of Deerness recapture surveys in summer 2014, used to investigate summer-time dispersal of trout parr.

Following the initial PIT-tagging of trout parr at sites along the Deerness, recapture sessions during the summer of 2014 enabled the re-sampling of individuals to determine their level of movement. Three single-pass electrofishing surveys were conducted at each site in contiguous stop-netted 20 m stream sections over a period of *ca.* two months (early July to mid September 2014). The distance surveyed was increased in each session from initially 100 m to finally 200 m upstream and downstream of each starting point. During the first recapture session at sites T2, T3 and T4, and during the first two recapture sessions at sites T1, T5 and T6, any untagged individuals captured were tagged and subsequently released back into the population. The frequencies of maximum longitudinal distances covered by each recaptured fish from a previous site of release showed a typical inverse-power distribution. Following the methods of Bubb et al. (2004), linear transformation using a double-ln plot enabled regression analysis. Upstream and downstream dispersal were analysed separately and the regression lines compared. To maximise sample size, the recorded dispersal ranges were combined from all study sites.

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Online Resource 2: Investigating the phenology of downstream migration in juvenile trout.

Results and analysis of the Deerness recapture surveys of trout parr dispersal in summer 2014.

A total number of 330 fish were recaptured during single pass recapture surveys on the Deerness between late July and mid-September 2014. The maximum distance covered by any one trout tagged and recaptured within the same Deerness study site, July to September 2014, was 260 m, however many recaptured individuals (50.2%) remained within the 20m zone in which they were first released, and the majority (83.0%) travelled no further than 60m from previous known locations (Fig. S1). The probability, *M*, of moving a dispersal distance of *D* m was described by an inverse-power function using the inverse cumulative proportion of dispersers in each 20 m sample zone from the site of release (Bubb et al. 2004):

$$M = CD^{-n}$$

C and *n* are scaling constants. A highly significant negative relationship between ln*M*, both upstream and downstream, and ln*D* was found (Upstream: $F_{1, 7} = 82.7$, $p < 0.001$, $R^2 = 0.92$; Downstream: $F_{1, 10} = 121.7$, $p < 0.001$, $R^2 = 0.92$; Fig. S2) under the equations:

$$\ln M \text{ (upstream)} = 7.25 - 2.26(\ln D)$$

$$\ln M \text{ (downstream)} = 7.22 - 2.21(\ln D)$$

No significant difference between the gradients of the two regression lines was found ($t_{20} = -0.18$, $p = 0.86$), meaning trout were equally likely to disperse upstream and downstream (Fig. S2).

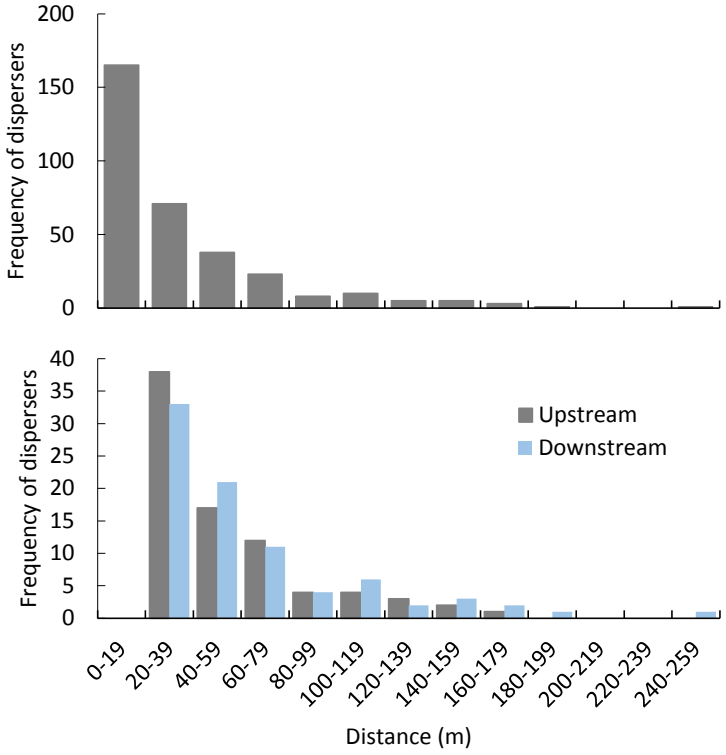

Fig. S1: Frequency distribution of the maximum longitudinal movements made by trout from a previous release site (top), with upstream and downstream movements separated (bottom), all study sites combined.

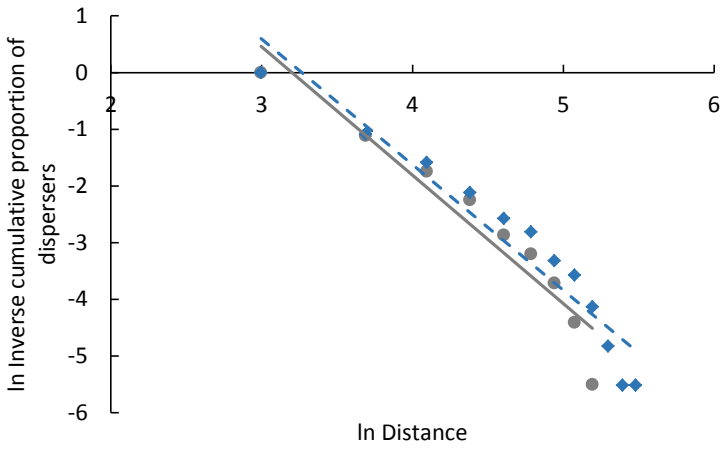

Fig. S2: Double-ln plot of the inverse cumulative proportion of dispersers in upstream (grey) and downstream (blue) directions.

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653 **References**

654 Bubb, D. H., T. J. Thom & M. C. Lucas, 2004. Movement and dispersal of the invasive signal crayfish
655 *Pacifastacus leniusculus* in upland rivers. Freshwater Biology, 49: 357-368.

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